[Reprinted from PSYCHIATRIC RESEARCH REPORTS 6,
AMERICAN PSYCHIATRIC ASSOCIATION, October 1956]

1956
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EXPERIMENTS ON PERCEPTUAL INTEGRATION IN ANIMALS *

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I SHALL try to present a brief over-all glimpse of some of the things we have been doing in efforts to learn more about the cerebral mechanisms underlying perception, perceptual learning, and perceptual memory.

The first work I shall mention deals with a brain theory of perception that developed out of the Gestalt school of psychology, and is perhaps most commonly referred to as the "electrical field theory of cerebral integration." Proponents of field theory have ascribed a primary role in brain function to gross electric currents that spread through the cortex *en masse;* that is, through the cortical tissue as a volume conductor. They suggest that most aspects of perception are more satisfactorily correlated with these gross electric currents in the brain than with the more orthodox type of nerve impulses that travel in scattered discontinuous patterns along discrete fiber pathways.

Figure 1 is taken from an experiment [1] aimed at testing this electrical field theory. The visual area of the cortex in the cat was filled with metallic inserts of tantalum wire, as shown in this X-ray picture of the brain of one of a group of 3 cases. The aim here was to short circuit and hence to distort the normal patterning of DC current flow in the cortex during visual form perception. These numerous metallic inserts proved to have no measurable effect on previously trained, high level pattern discriminations.

Figure 2 is from another experiment also aimed at testing the electric

* Work included in this report has been supported by the F. P. Hixon Fund of the California Institute of Technology and by grants from the Mental Health Foundation of Southern California and the National Science Foundation.

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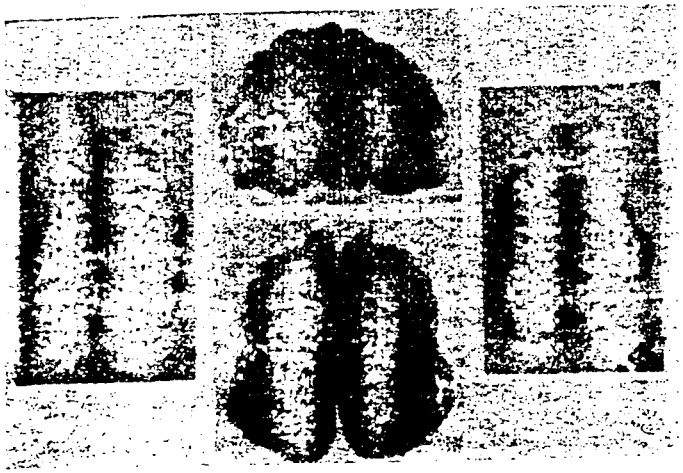

FIGURE 1.

field theory.[4] In this case the approach was just the opposite, the conclusion just the same. The dashes represent dielectric or insulating plates of mica inserted vertically into the gray matter of the cortex. Again, the aim was to distort, this time by blocking instead of by shorting, the postulated patterns of DC flow in the visual area during pattern perception.

The next figure, Figure 3, shows a surface view of one of the brains after removal and X-ray views of the same brain. In this experiment there was very little functional deficit so long as the mica inserts were restricted to the depth of the gray matter. When the inserts went deep into the white matter, as shown here, there was considerable impairment which, however, was largely corrected in the course of two and one-half months. Where functional impairment was found, it appeared to be correlated with the tissue damage produced by the inserts and not by their dielectric effects. In no case were the post-operative deficits any greater than those produced by knife cuts made in the same pattern to simulate the tissue damage of the inserts without their dielectric effects.

The outcome of these two studies has rather discouraged any inclination, on our part at least, to forsake the traditional fiber conduction doctrine of brain function in favor of the newer electrical field hypothesis.

Any brain theory of perception, we believe, must square also with the following observation: The visual area of the cortex, in the cat again, was sliced with numerous subpial knife cuts in criss-cross patterns [5] as shown in Figure 4. When patterns of knife cuts, as shown in the top two cases, proved

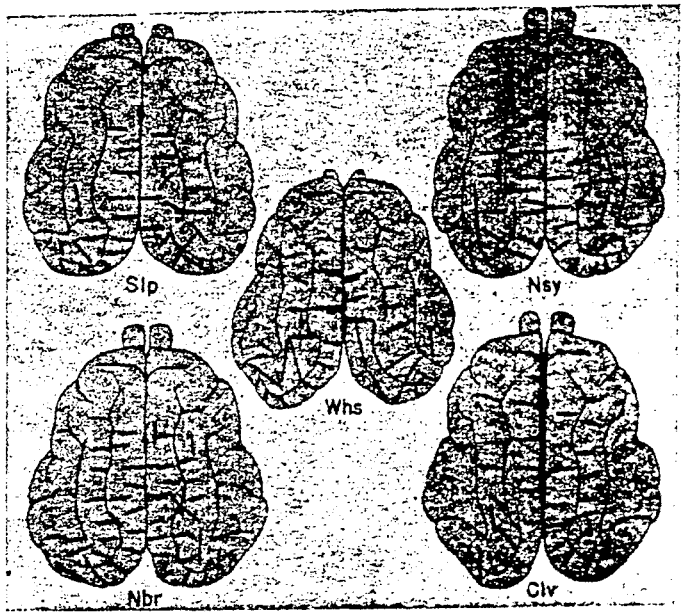

FIGURE 2.

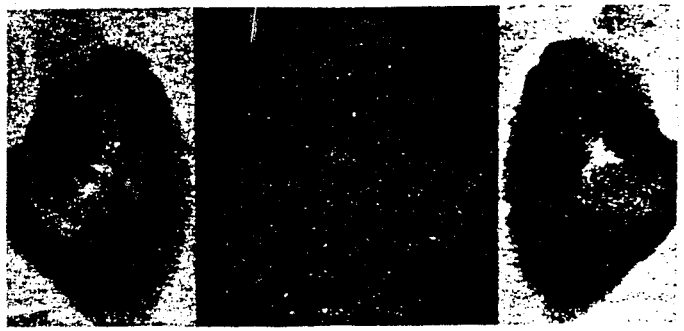

FIGURE 3.

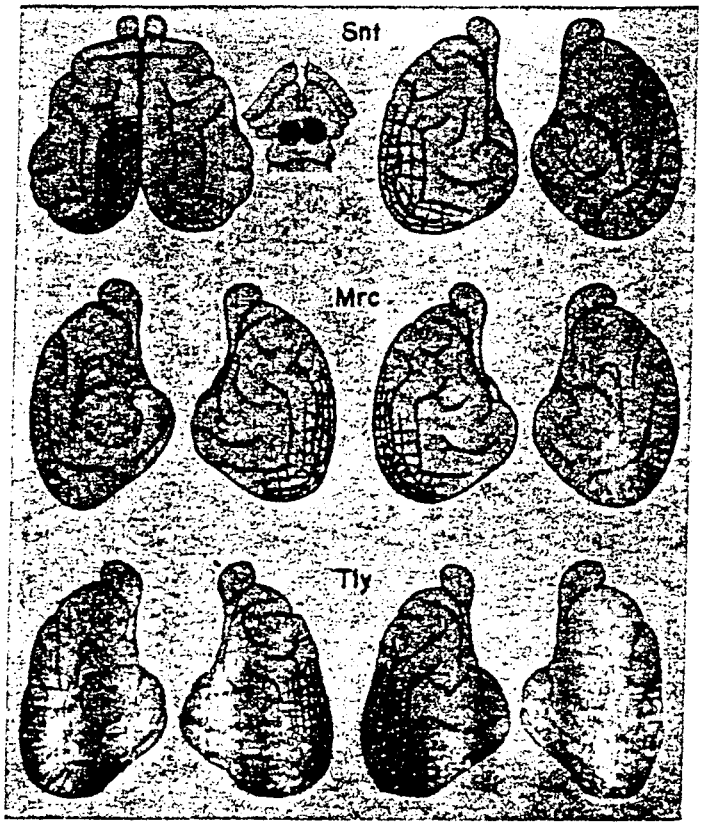

FIGURE 4.

to have only negligible effects upon pattern perception, we decided in the third case to carry this slicing procedure to an extreme, making the cuts as numerous and as close together as possible. Figure 5 shows a surface view of the removed brain of this third, extreme case. At the end of the three and a half hour operation the sliced area on both sides in this third case was swollen and cyanotic, and looked as if it would never function again. This animal was completely blind the first four days after operation. On the fifth day vision began to come back, and by the fourth week this animal was performing again on our test scales at a level only one or two notches below its preoperative level.

FIGURE 5.

On the left in Figure 6 is shown the best discriminations that this animal was able to achieve after operation. It could discriminate the central triangle when paired with any of those shown surrounding it. And it readily learned the size discrimination shown on the right. The results of this slicing procedure seem to eliminate as an important factor in perceptual integration the tangential or horizontal spread of cortical conduction within the gray matter, that is, on any scale large enough to mediate so-called relational or structuring effects in perception.

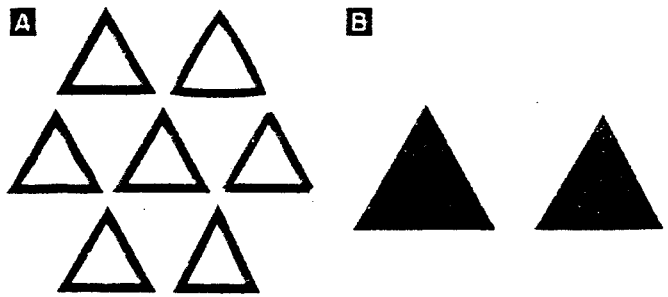

FIGURE 6.

The remaining studies that I am going to touch on are concerned with the function in perception of the long association fiber systems of the cerebral hemispheres. In work conducted largely by Dr. Myers it has been possible to demonstrate an important integrative function for the corpus callosum.[1, 2, 6] As you may recall, extensive testing of human patients with complete callosal section has failed to reveal any clear-cut functional symptoms associated with damage to this largest of all the fiber tracts in the human brain.

In these animal experiments, the optic chiasma is first sectioned in the midline to restrict the input from each eye to the ipsilateral side of the brain (Figure 7). The animals are then taught a few simple visual discriminations with a mask over one eye. After the habit has been stablized by overtraining, the mask is shifted to the other eye. Under these conditions we find that the trained performance transfers readily to the untrained eye, provided the corpus callosum is intact. If the corpus callosum has been sectioned prior to the training, there is no transfer whatever. Without the corpus callosum, such animals apparently have no recollection with one eye of what they have been doing with the other eye. In fact, it is possible to train opposing incompatible discriminations to the separate eyes without any interference between the two patterns.

More recently, in collaboration with Dr. Stamm, we have obtained similar results for the contralateral transfer from one forepaw to the other of tactile discriminations.[7] The cats are trained to push the correct one of two pedals which they are unable to see and must distinguish entirely on the basis of touch. One gets 70 to 80 per cent transfer of learning upon shifting to the untrained paw in cats that have the corpus callosum intact. The transfer is zero with the corpus callosum sectioned.

Perceptual learning and memory thus seem to proceed quite independently in the two hemispheres in the absence of the callosum. It is interesting that

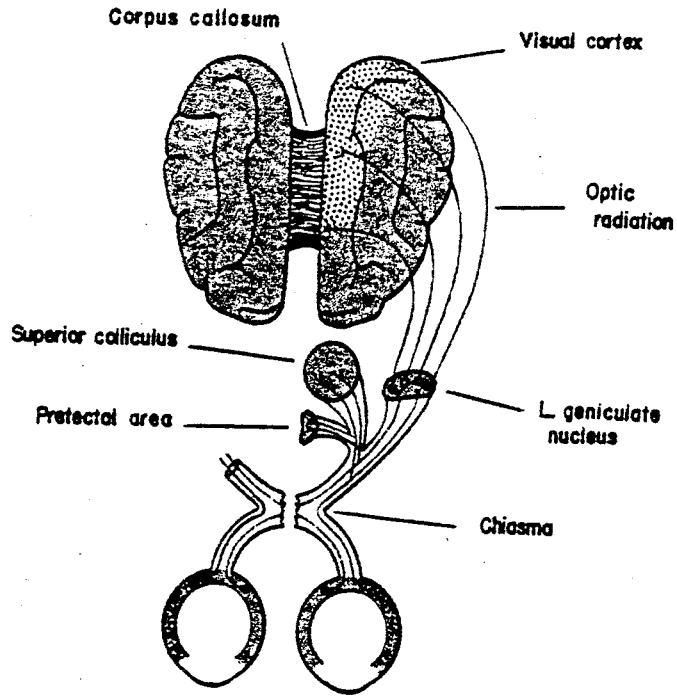

FIGURE 7.

in spite of this independence, the learning process in the two separated hemispheres is remarkably similar in character as judged by the close matching of the learning curves for the two hemispheres. If one plots the learning curves for a series of cats on the same problem, one finds considerable variation. Also, the curves for the same individual on different problems will vary considerably. The fact that this kind of variation tends to run parallel in the two separated hemispheres suggests that the individual variability in perceptual learning is not a reflection merely of accidental and fortuitous aspects of the learning process and the general learning situation, but is predetermined to a surprising degree by the intrinsic structural and functional organization of the cerebral hemisphere. We have obtained this same result for tactile as well as for visual discriminations.

With respect to the old problem of the localization in the brain of memory traces, it is interesting that one can excise the visual and neighboring asso-

ciation cortex plus the auditory field and the entire temporal lobe on the trained side in these animals before switching the mask and still get the transfer to the untrained eye through the callosum.[2] One can also get transfer of simple discriminations if the entire callosum is sectioned, after the completion of training, but before testing for the transfer. This shows that the memory traces ingrained, for these habits are not confined to the sensory receiving area of the cortex. Some kind of mnemonic carryover into the opposite hemisphere is effected via the corpus callosum.

Currently we are investigating the functional capacities of isolated remnants of cortex. In these studies we are putting to use the demonstrated functional independence of the two hemispheres in what we have come to call the "split brain preparation." This is an animal in which the brain has been split down the middle by section of the corpus callosum and hippocampal commissure and usually also the optic chiasma and anterior commissure. Incidentally, such animals are indistinguishable from normal to casual examination.

In these split brain animals, the brain lesion analyses are being carried out in one hemisphere alone.[3] The other hemisphere is preserved intact to prevent incapacitating paralyses and to maintain generalized background functions. In the test hemisphere, instead of the customary small lesions in the critical area, it becomes possible under these conditions to use the converse approach, that is, to remove the greater part of the cortex leaving intact only that critical area which one wishes to test. The functional tests, of course, must be unilateral. When the occipito-visual area is isolated in the manner shown in Figure 8, all previously trained visual discriminations tend to be lost. But, the very simplest discriminations, such as that between horizontal and vertical striations, may survive in part in the exceptional case and these can be retrained, though not easily. Postmortem histological checks indicate that the severe visual impairment is not attributable to geniculostriate damage.

The results have been different in the case of tactile perception, where we are finding good retention of previously trained habits and good learning of new tactile discriminations with only a small island of frontal cortex left intact including the somatic area as shown in Figure 9. Apparently we are approaching the minimum here, however, because the most difficult discrimination, which was a sandpaper versus a smooth surface, was only partially retained in two of four cases, although it could be re-learned. Subsequent destruction of the intact cortical island, or removal of the same cortical area from the opposite hemisphere, abolished in either case all further discrimination with the respective contralateral forepaw.

This is about where we stand at present. As you can see, we are still miles away from being able to draw up any detailed circuit diagrams for per-

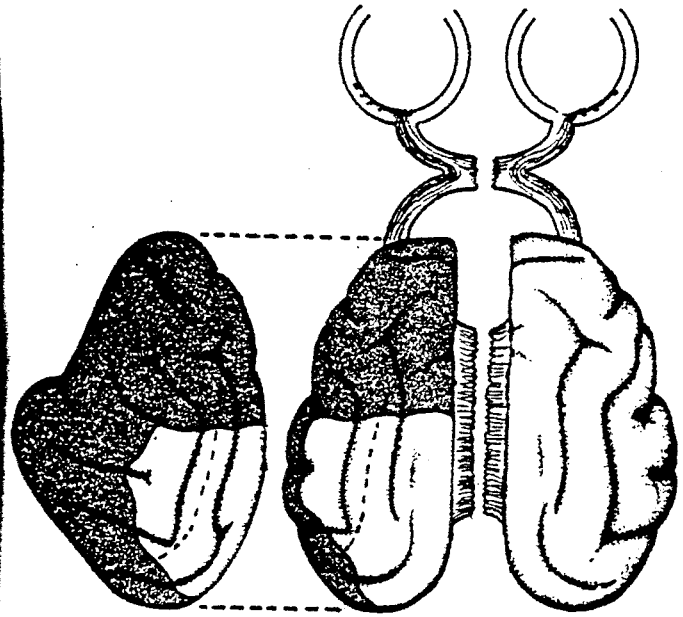

FIGURE 8.

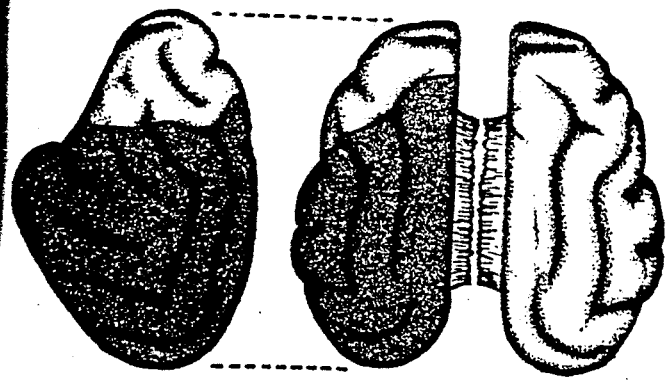

FIGURE 9.

ceptual learning and memory. As far as we are concerned, the recourse in psychiatry to use of the term "brain mythology" still remains all too justified.

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